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EVOLUTIONARY TRENDS IN DENTAL MORPHOLOGY OF THE GENUS *PROLAGUS* (OCHOTONIDAE, LAGOMORPHA) IN THE MEDITERRANEAN ISLANDS

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Resum

Igual que altres taxa de vertebrats, el gènere *Prolagus* va sofrir modificacions morfo-funcionals importants als ambients insulars mediterranis. El més evident és un increment al·lomètric de la mida general, seguit per altres canvis notables a nivell dentari: increment de la hipsodòncia i del nivell de complexitat de plegament de l'esmalt, i modificacions de les proporcions de diversos trets dentaris. Aquests canvis peculiars es podrien explicar com a adaptacions paral·leles a ambients oberts secs, amb una vegetació molt dura i amb pressions de depredació baixes. Esdevenen a totes les espècies endèmiques de *Prolagus* diferenciades a ambients insulars mediterranis, fins i tot encara que no tinguin un ancestre directe comú. Algunes formes europees continentals poden mostrar algunes de les característiques esmentades (per exemple, només gegantisme o només presència d'esmalt dentari molt plegat) degut a adaptacions locals alimentàries o ambientals. Només la presència conjunta dels trets dalt esmentats identifica les espècies de *Prolagus* insulars.

Paraules clau: *Prolagus*, insularitat, endemisme, adaptacions ambientals/alimentàries, illes mediterrànies.

Abstract

As other vertebrate *taxa*, genus *Prolagus* undergoes major morpho-dimensional modifications in Mediterranean insular environments. The most evident is an allometric general size increase, followed by other remarkable changes at the dental level: increase of hypsodonty and of enamel folding complexity, modification of relative proportions of some dental features. Such peculiar changes could be explained by a parallel adaptation to dry, open environments with harder vegetation and by a minor predatory pressure. They occur in all the *Prolagus* endemic species differentiated in insular Mediterranean environments, even if they do not share a common direct ancestor. Some continental European forms, actually, can show some of the listed features (e.g.: giantism only, or highly folded dental enamel only) due to particular dietary/environmental local adaptations. Only the coincident occurrence of the above mentioned characters identifies an insular endemic *Prolagus* species.

Key Words: *Prolagus*, insularity, endemism, environmental/dietary adaptations, Mediterranean islands.

INTRODUCTION

Lagomorphs, and especially the genus *Prolagus* among them, are quite well represented in Mediterranean insular faunal assemblages. Nevertheless, they were object of very few specific works (Major, 1882; Tobien, 1935; López Martínez & Thaler, 1975) and except for López Martínez (1978) no modelization and/or explanation for the morpho-dimensional changes they undergo in insular domains does exist so far.

Lagomorph fossil findings are usually included in micromammalian lists, even if their size, habits and escaping strategies differ quite markedly from that of the bulk of micromammals, but they can not be considered as macromammals either. So, verifying which pattern of morpho-dimensional modifications (the macromammalian one, the micromammalian one, or a patchwork of the two) will a lagomorph follow as a response to the permanence in an insular environment is the main aim of this paper.

The genus *Prolagus* is one of the three representatives of the family Ochotonidae found in insular environments of the Mediterranean area up to now. The others are *Gymnesicolagus gelaberti* Mein & Adrover (Santa Margalida, Mallorca, Middle Miocene; Mein & Adrover, 1982) and *Paludotona etruria* Dawson (Baccinello V1 - and two related forms both named *Paludotona* aff. *P. etruria* in levels V0 and V2 -, Western central Italy, MN11-basal MN13; Dawson, 1959; Kotsakis *et al.*, 1997). The following endemic insular *Prolagus* species have been differentiated in Mediterranean insular domains (Fig. 1): *Prolagus apricenicus* Mazza and *P. imperialis* Mazza from the Gargano Peninsula (South-Eastern Italy, MN13/14;

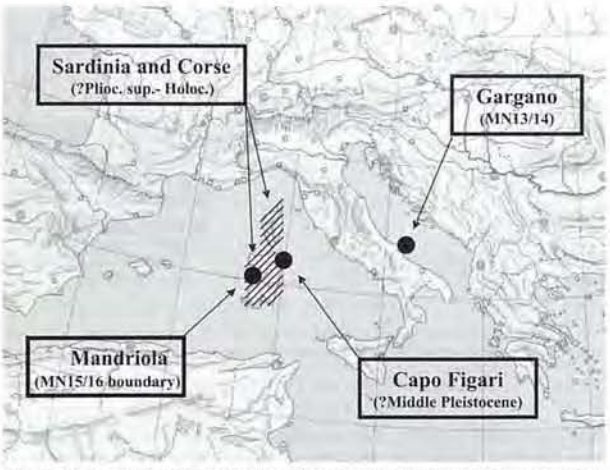


Fig. 1. Geographical localization of endemic insular *Prolagus*-bearing fossiliferous sites in the Mediterranean area.

Fig. 1. Localització geogràfica de les localitats que han lliurat Prolagus *endèmics insulars a l'àrea mediterrània.*

Mazza, 1986a, 1986b, 1987), a probable new species, *Prolagus* aff. *P. depereti* from Mandriola (Western Sardinia, MN15/MN16 boundary; Angelone & Kotsakis, 2000), *P. figaro* Lopez Martinez from Capo Figari (Eastern Sardinia, ?Early/Middle Pleistocene; López Martínez & Thaler, 1975) and *P. sardus* (Wagner) found in several fossiliferous sites in Sardinia and Corsica (Pleistocene-Recent). These species show marked morphological and dimensional modifications due to the permanence in insular environments.

Such morpho-dimensional modifications clearly lack in *Prolagus* species found in present-day insular environments that in the past were connected to mainland, as testified by the presence of continental, well-balanced, fossil faunal assemblages with non-endemic faunal elements: *Prolagus* sp. from Thymiana (Chios, Greece, MN8; Tobien, 1968), *Prolagus* sp. from N Katheni (Evia, Greece, ?MN10; Katsikatsos *et al.*, 1981), *P.* cf. *P. michauxi* Lopez Martinez from Aghios Ioannis (Karpathos, Greece, MN14; Daams & Weerd, 1980), *Prolagus* cf. *P. calpensis* Major from Medes Islands (Spain, Pleistocene; López Martínez, 1989), *P. "corsicanus"* Giebel from Ratonneau Island (France, Pleistocene; Piveteau, 1961). For this reason those species will not be taken into consideration here.

Moreover, as only the morpho-dimensional aspects of insular endemic *Prolagus* species (that, as will be demonstrated, are shared by all the considered species) are discussed here, open systematic discussion, as the presence in the Mandriola fossiliferous site of two distinct and may be heterochronical *Prolagus* species, or the existence of intermediate morphotypes between *P. sardus* and *P. figaro* in the Monte Tuttavista (Orosei, Eastern Sardinia, Italy; ?Late Pliocene-Late Pleistocene) fissure fillings that cast a doubt on the actual separation between the two species, shall be avoided here.

Materials and Methods

Fossil remains of *Prolagus*, as it occurs for micromammals in general, mainly consist in dental and secondarily in maxillary and mandibular elements; cranial and postcranial remains are quite rare and/or ill-pre-

Species	D_1 (anteroconid)	D_2 (posterior complex)	D (D_1+D_2)
Prolagus oeningensis	1.15	5.56	6.71
Prolagus major	1.17	5.28	6.45
Ptychoprolagus forsthartensis	1.22	5.84	7.06
Prolagus tobieni	1.35	3.92	5.27
Prolagus michauxi	1.11	4.50	5.61
Prolagus depereti	1.30	5.86	7.16
Prolagus cf. *P. calpensis* (Moreda)	1.16	4.82	5.98
Prolagus cf. *P. calpensis* (I. Medas)	1.52	5.57	7.09
Prolagus aff. *P. depereti*	1.52	-	-
Prolagus sardus	1.42	4.93	6.35
Prolagus cf. *P. sardus* (Orosei)	1.37	5.22	6.59
Prolagus figaro	1.51	6.20	7.71
Prolagus apricenicus	1.77	6.55	8.32
Prolagus imperialis	2.23	7.61	9.84

Table 1. Density indexes (Dn=L/4πF, where L is enamel length, F the area inclosed by the enamel including enamel thickness+dentine; Schmidt-Kittler, 1986) calculated on different elements of various *Prolagus* species P_3 occlusal surface. D_1: anteroconid; D_2: extant part of P_3 enamel portion; D: D_1 + D_2.

***Taula 1.** Índex de densitat (Dn=L/4πF, on L és la llargària de l'esmalt, F l'àrea inclosa per l'esmalt, icomptand el gruix de l'esmalt + la dentina; Schmidt-Kittler, 1986) calculats sobre diferents elements de la superfície oclusiva del P_3 de diverses espècies de Prolagus. D_1: anterocònid; D_2: part existent de la porció d'esmalt del P_3 ; D: D_1 + D_2.*

served. In order to make the results of this paper applicable in the majority of the cases, comparisons between continental and insular endemic *Prolagus* species have been made on the basis of dental findings.

P_3 is still now considered to be the most significant dental element for systematics at the species level for the genus *Prolagus*. For this reason most of the morphodimensional analyses carried out to individuate advanced characters shared by insular endemic *Prolagus* species have been made on P_3 (see López Martínez, 1989, for nomenclature).

It has been possible to recover fossil material of each of the insular endemic above mentioned *Prolagus* species that has been compared morphologically and dimensionally with European continental species and populations.

Results

Dental modifications observed in insular endemic *Prolagus* species of the Mediterranean area are the following:

Size increase

The first, most evident feature that characterizes endemic insular *Prolagus* species, if compared with European continental ones, is size increase (Fig. 2). Size increase of mandibles, cranium and postcranium is surely allometric, but it deserves a more complete and complex discussion and is for the moment excluded: actually, the extreme scarcity of available postcranial elements in almost all European fossil sites bearing *Prolagus* makes osteological comparisons problematic.

Dental size increase, in comparison with coeval European continental species, is rather considerable in *P. apricenicus* and *P. imperialis* from the Gargano fossil archipelago, not so striking in Corso-Sardinian species. Actually, in Messinian times, a very sharp shift occurs in size and dental morphology of continental Europe *Prolagus*: primitive, small *Prolagus* species disappear to be replaced almost everywhere by *P. michauxi*. This species is quite big-sized, and in its dental morphology attains many features till then shown by Gargano insular endemic *Prolagus* species only, as a triangular, lingually-shifted anteroconid on P_3 and the presence of a mesial hyperlophe on P^2. As a matter of fact, a kind of mesial hyperlophe on P^2 has been observed (in species more

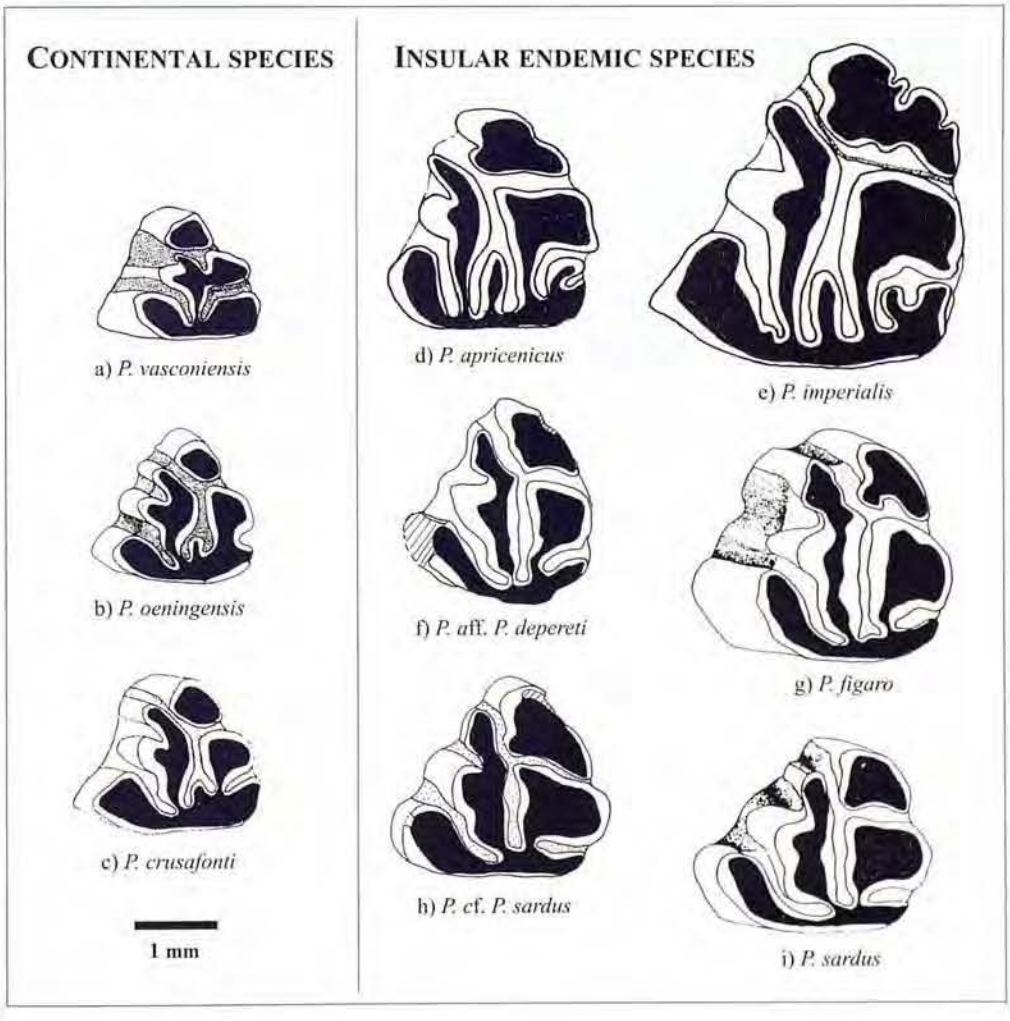
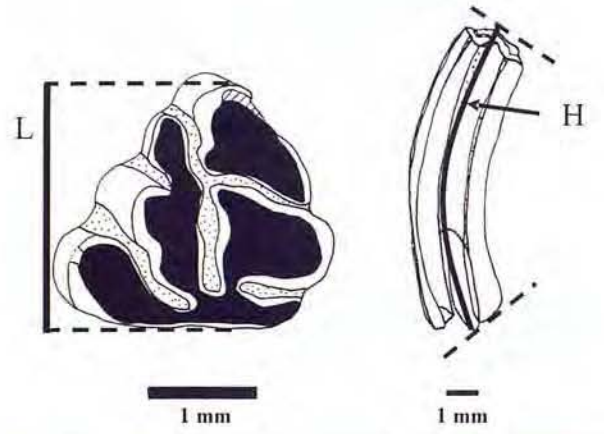


Fig. 2. Comparison of P_3 size between some continental non-endemic species and insular endemic species of genus *Prolagus*. Drawings from López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) and from unpublished data of the author.

Fig. 2. Comparació de la mida del P_3 entre algunes espècies no endèmiques continentals i espècies endèmiques insulars del gènere Prolagus. *Dibuixos a partir de López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) i de dades no publicades de l'autora.*

ancient than *P. michauxi*) only in two specimens of a very large population of advanced *P. crusafonti* (López Martínez, 1989); it could be also observed in *Ptychoprolagus forsthartensis* Tobien (that in spite of the generic differentiation, due to its very peculiar appearance, can be legitimately considered as a *Prolagus* species), whose extremely limited distribution in time and space (Forsthart, Southern Germany, Middle Miocene; Tobien, 1975) and whose singular occlusal surface features, attest to a continental endemic condition and to an adaptation to particular environmental conditions (Fig. 4).



Species	L (mm)	H (mm)	I=H/L
Prolagus schnaitheimensis	1.80	6.35	3.53
Prolagus tobieni	1.46	6.30	4.31
Prolagus vasconiensis	1.47	6.72	4.57
Prolagus ibericus	1.38	6.38	4.62
Prolagus oeningensis	1.51	7.09	4.69
Prolagus cf. *P. michauxi*	1.85	8.38	4.53
Prolagus aff. *P. depereti*	2.42	-	-
Prolagus apricenicus	2.36	11.17	4.73
Prolagus imperialis	2.99	14.43	4.83
Prolagus figaro	2.05	9.30	4.53
Prolagus cf. *P. sardus*	2.07	13.10	6.33

Fig. 3. Definition of hypsodonty ratio I = H/L. H is absolute hypsodonty measured in lateral-labial sight from the anteroconid to the lowest part of the tooth (more or less along the protoflexid or protoconid); if the available dental elements are broken in their central lower part, H can be estimated as shown. L is the lenght of the tooth measured on its occlusal part. I ratio, here illustrated for P_3, can be calculated in the same way on other teeth.
In the table: Comparison of P_3 occlusal lenght (L) and absolute hypsodonty values (H) of some selected european continental and endemic insular *Prolagus* specimens. Hypsodonty degree (I) is the result of the H/L ratio.

Fig. 3. Definició de l'índex d'hipsodòncia I = H/L. H és la hipsodòncia absoluta, mesurada en norma lateral – labial, des de l'anterocònid a la part més baixa de la dent (més o menys, al llarg del protoflèxid o protocònid); si els elements dentaris disponibles es troben trencats a la seva part central, es pot estimar H així com es mostra. L és la llargària de la dent mesurada a la seva part oclusiva. L'índex I, que aquí s'il·lustra per al P_3, es pot calcular d'una manera similar per a les altres dents.
***A la taula:** comparació de la llargària oclusiva del P_3 (L) i els valors d'hipsodòncia absoluta (H) d'alguns espècimens seleccionats de* Prolagus *continentals i endèmics insulars.*

In P_3, the dental element in which specific differences can be more easily recognized, the percentage of lenght (L) increase measured on occlusal surface can reach values higher than 100% (*P. praevasconiensis* Ringeade / *P. imperialis* Mazza). Width is a character that can vary in a remarkable way through ontogeny, so is less fiable for size increase estimations.

The percentage of size increase between continental ancestor and insular endemic descendant is very variable. A size increase of about 50-60% and 100% can be observed in P_3 between *P. oeningensis* and its endemic descendants *P. apricenicus* and *P. imperialis* respectively (Fig. 2); if we consider *P. figaro* as a descendant of *P. depereti*, the size increase of the former is of about 12% only. The same percentage of size increase (about 11%) has been calculated between *P. sardus* and its supposed continental ancestor *P. calpensis*. If size increase percentage calculation is made using *P. michauxi* as continental point of re-ference (actually both *P. depereti* and *P. calpensis* descend from *P. michauxi*), its value grows slightly.

Hypsodonty increase

Increase of absolute hypsodonty of insular endemic *Prolagus* is a natural consequence of the increase of overall size. The hypsodonty degree (I), here meaning the H/L ratio (Fig. 3), has been introduced to verify if hypsodonty increase is just a direct consequence of P_3 overall increase or if there is another component. In insular endemic *Prolagus* species the ratio I is higher (tab. 1), but is very variable and no clear hypsodonty increasing pattern can be deduced: to bigger occlusal surface size do not correspond biggest I ratios (Garganic *Prolagus*, the biggest insular endemic species, have the lowest I ratio).

This character should be further investigated and modelized, such as P_3 radius of curvature: in general, primitive *Prolagus*, such as *P. vasconiensis*, *P. schnaitheimensis*, *P. tobieni*, in most cases appear to be quite straight in lateral lingual or labial view (but they can appear bent on a lateral antero/posterior view), while even slightly more advanced forms (as *P. oeningensis*) or insular endemic *Prolagus* species appear to be curved in lateral lingual view.

Modification of dental occlusal surface

Major modifications of insular endemic *Prolagus* species dentition occur on P_3. Extant lower dental elements have a very conservative morphology. Upper molars do not show remarkable change either, if compared to those of continental non-endemic species. P^2 and P^3, that are in occlusion with P_3, appear to be bulky and massive, with a higher L/W ratio; moreover in P^2 can be observed some more complex modifications (Fig. 4), as the undulations in the lagicone and in the postcone and as the presence of a very developed mesial hyperlophe (also in the most ancient known insular endemic species, *P. apricenicus* an isolated precone is not a common feature). The connection precone-mesial hypercone (mesial hyperlophe) appears in continental Europe

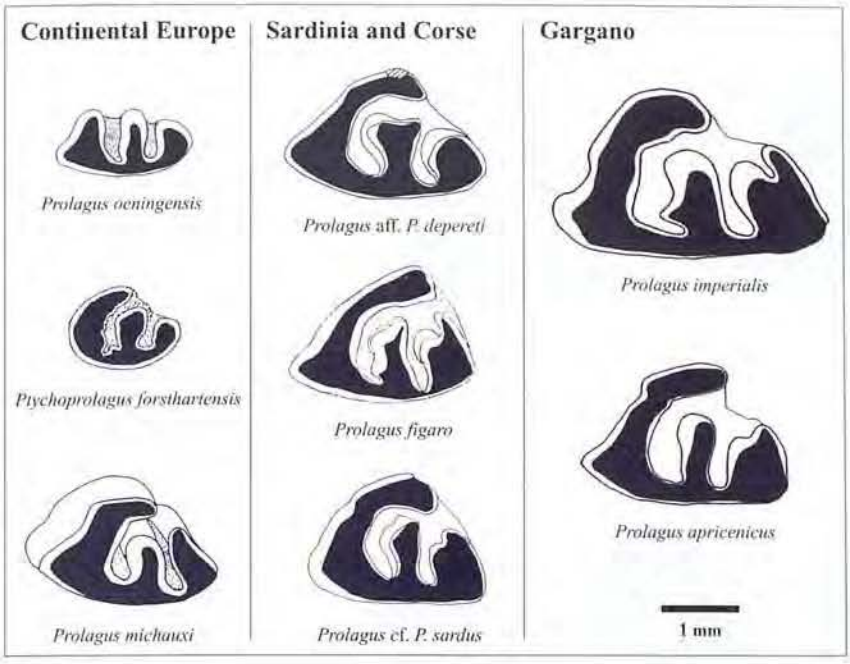


Fig. 4. Comparison of P^4 occlusal surface morphology. In insular endemic species the mesial hyperlophe is present and enamel on lagicone and postcone may be folded. In primitive *Prolagus* species of continental Europe, as *P. oeningensis, P. crusafonti,* etc., such features are not present: they appear in latest Neogene with *P. michauxi* and its descendants (*P. calpensis, P. depereti,* etc.). Drawings from López Martínez & Thaler (1975), Ziegler & Fahlbusch (1986), Mazza (1987), López Martínez (1989) and from unpublished data of the author.

Fig. 4. Comparació de la morfologia de la superfície oclusiva del P^4. A les espècies endèmiques insulars l'hiperlof mesial és present, i l'esmalt del lagiconus i postconus pot estar plegat. A les espècies primitives de Prolagus *d'Europa continental, tals com* P. oeningensis, P. crusafonti, *etc., no es troben aquests trets: apareixen al Neògen més tardà amb* P. michauxi *i els seus descendents (*P. calpensis, P. depereti, *etc.). Dibuixos a partir de López Martínez & Thaler (1975), Ziegler & Fahlbusch (1986), Mazza (1987), López Martínez (1989) i de dades no publicades de l'autora.*

with *P. michauxi* (late MN12-MN16). Corso-Sardinian *Prolagus* species, as advanced continental ones derived from *P. michauxi*, still retain this feature of their ancestor, while in the Gargano this character appears independently and is due to a convergence phenomenon.

P_3 modifications (Fig. 5) are more complex and deserve a more ample discussion. As already noticed by López Martínez (1978), P_3 anteroconids of insular endemic species appear to have a peculiar indented contour; moreover they become larger than in pre-Pliocene continental species, triangular, elongated and shifted towards the lingual side. Enamel folding complexity increases all over P_3 occlusal surface, even in different degrees in each species. The metaconids of insular endemic *Prolagus* species become larger and quadrangular in shape. The posterior portion of P_3 (entoconid + basal part of hypoconid), on the contrary, becomes much thinner. In general, overall shape of P_3 changes, assuming a quadrangular instead of an approximately triangular shape, due to the enlargement of the anterior side.

A tentative to quantitatively esteem and compare P_3 enamel folding degree has been made (tab. 1) by calculating two density indexes (Schmidt-Kittler, 1986): D1, considering the anteroconid only, and D2, considering the extant part of the tooth. Such density indexes do not express any information about shape similarity, but only about how much the perimeter of the selected dental element increases with respect to its area. As in this case the perimeter represents enamel lenght and development, its increase with respect to enclosed area (here representing dentine+enamel thickness), expressed by D index, indicates how much grin-ding surface increases. Thus, D index values and variations may have a dietary/environmental meaning and may possibly give hints about environmental and climatic changes.

In general, in *Prolagus* species D1 slightly increases with time in continental species and is higher in insular endemic ones. In *P. tobieni* D1 values are rather high, out of the average of continental *Prolagus* species, due to its flattened anteroconid, but D2 value is quite low; anyway, their sum D (D1+D2) falls between the values shown by continental species. *P. tobieni* has a very primitive post-anteroconid structure, still showing a centrolophid instead of a centroflexid, as more advanced species do: maybe a differential enamel lenght increase localized in the anteroconid supplied to the need of a higher grinding surface, attained in continental species from *P. oeningensis* on with the developing of a centroflexid, the growth of the protoconulid and the appearance of structures as the crochet.

D2 (post-anteroconid density index) does not show an equal increase with time in continental European *Prolagus* species and it is evidently higher in *P. figaro, P. apricenicus, P. imperialis,* but not in *P. sardus* (unfortunately no data of *P.* aff. *P. depereti* are available).

It is worth to remark also a differential size increase of P_3 in comparison with the rest of the mandibular row. Mazza & Zafonte (1987) evidenced that in Garganic *Prolagus* species the highest muscle resultant during mastication is applied on P_3 that becomes the most important dental element for chewing. A difference in the dietary adaptation could have enhanced the stress on P_3: that could explain why it became more massive, increased its enamel folding complexity and underwent a further size increase in addition to an overall enlargement of the whole tooth row (Fig. 6).

Increased complexity of enamel folding noticed in insular endemic species is not a consequence of size increase, neither is in any way related to it. *Prolagus major* (late Early Miocene - early Middle Miocene), Calatayud-Teruel Basin, Spain; López Martínez, 1989), a giant European continental species, is comparable in size to insular species (Fig. 7), but shows no trace of enamel folding.

On the other hand, some continental European species show an increase of enamel folding complexity, but not a considerable size increase, such as the above

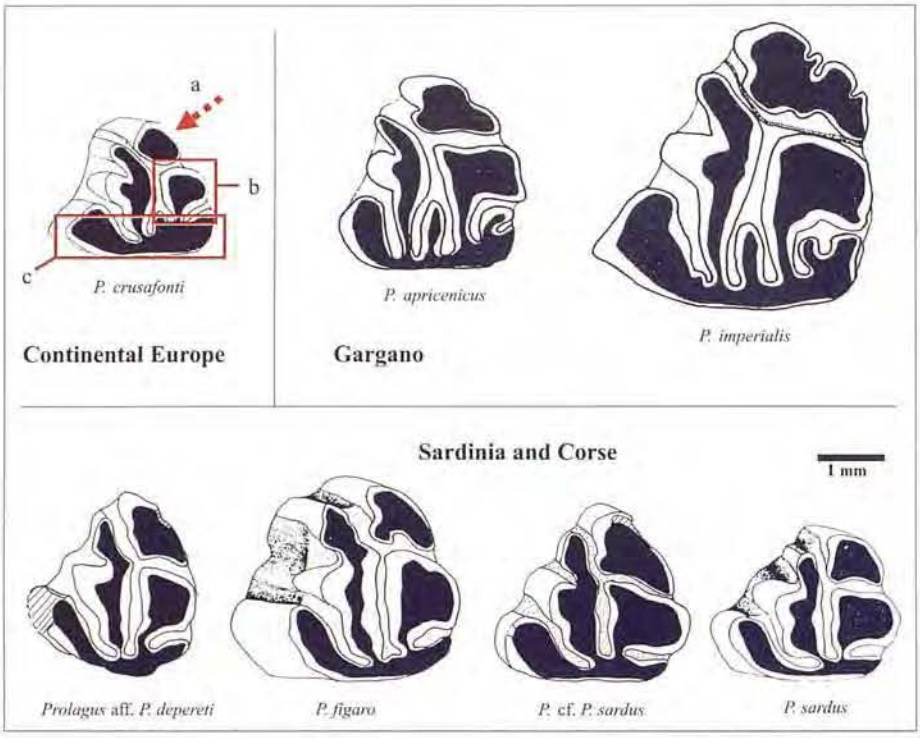


Fig. 5. Comparison of continental and insular endemic *Prolagus* P_3 occlusal surface morphology: a) anteroconid modifications (absent in continental species); b) metaconid shape and size (quadrangular and bigger in insular endemic species); c) size of the posterior part of the tooth (thinner in insular endemic species). Drawings from López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) and from unpublished data of the author).

Fig. 5. Comparació de les espècies continentals i endèmiques insulars de Prolagus. *Morfologia de la superfície oclusiva del P_3: a) modificacions de l'anterocònid (absents a les espècies continentals); b) forma i mida del metacònid (quadrangular i més gros a les espècies endèmiques insulars); c) mida de la part posterior de la dent (més robusta a les espècies endèmiques insulars). Dibuixos a partir de López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) i de dades no publicades de l'autora.*

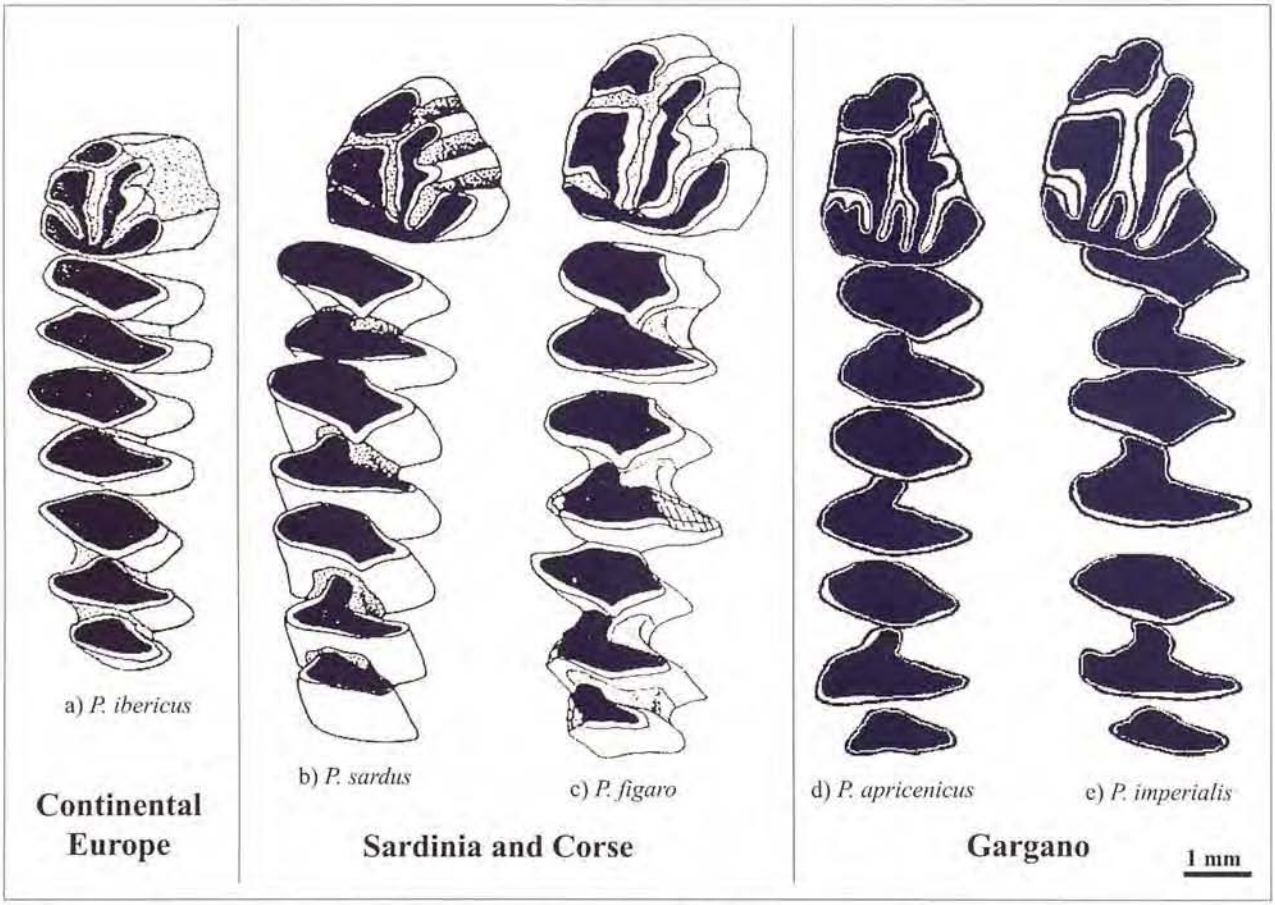


Fig. 6. Comparison of lower tooth rows of a non-endemic continental European species (a) and some endemic insular species. In insular endemic species the whole lower tooth row undergoes a slight overall size increase, while P_3 goes through a differencial, higher size increase, probable consequence of a change in mandibular mechanics. Drawings from López Martínez & Thaler (1975) and Mazza (1987).

Fig. 6. Comparació de les sèries dentàries inferiors d'espècies europees continentals no endèmiques (a) i algunes espècies endèmiques insulars. A les espècies endèmiques insulars tota la sèrie dentària inferior està afectada per un lleuger increment de la mida promig, mentre que el P_3 suporta un major increment diferencial de mida, conseqüència probable d'un canvi als mecanismes mandibulars. Dibuixos a partir de López Martínez & Thaler (1975) i Mazza (1987).

mentioned *Ptychoprolagus forsthartensis* and, in a lesser way, *Prolagus* cf. *P. calpensis* (Pliocene, Medes Islands, Spain; López Martínez, 1989). These species have a very limited geographical distribution, and this feature is probably due to particular environmental/dietary adaptations.

Therefore, only the contemporaneous occurrence of all the above listed characters individuates an insular endemic species.

Differentiation of *Prolagus* insular endemic species

In spite of all the common characters, it is possible to individuate some differences between the P_3 of endemic insular species, making possible the differentiation of two groups corresponding to Gargano species and to Corso-Sardinian ones (Fig. 8):

1 - in Gargano species, the anteroconid shows much more complex and marked indentations, and it is placed in a more "detached" position, giving to the tooth a more elongated, rectangular shape, while Corso-Sardinian forms have a more "compact", square appearance and a less elaborate anteroconid shape;

2 - in Corso-Sardinian species, the angle protoconid/protoconulid is wider (140-150 degrees against the 110-120 degrees of Gargano species),

3 - in Gargano species, enamel folding is more complex and occurs also in other points of the occlusal surface.

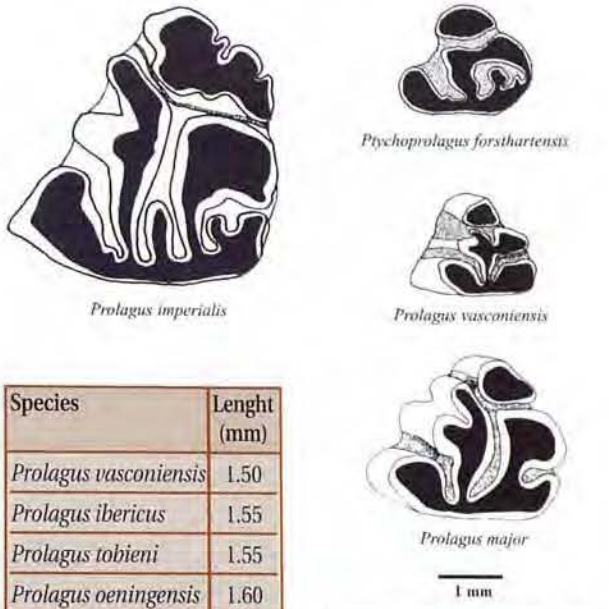
Discussion

Micromammalian pattern of evolution on islands

Micromammalian pattern of evolution on islands has been modelized (Azzaroli, 1982; Mein, 1983; Agustí, 1986) with the individuation of two main phases: a first stage, in which species undergo quite instantaneous modifications taking place immediately after the colonization of the island, followed by a slow anagenetic phase. The first phase is so sharp that it is very unlikely that it can be documented by fossils (an exception is *Rhagapodemus azzarolii*, Mandriola, Western Sardinia, MN15/16 boundary; Angelone & Kotsakis, 2001).

Prolagus pattern of evolution on islands

Members of genus *Prolagus* that populated insular environments followed in general micromammalian pattern of modifications in similar conditions. Actually, even in the bradytelic genus *Prolagus*, size increase, direct consequence of the scarcity of terrestrial predators, is attained in a quite instantaneous way: the oldest findings of Gargano *Prolagus* species already show a very big size and consequently a higher absolute hypsodonty; *Prolagus* aff. *P. depereti* is morphologically less developed, but as big as its descendant *P. figaro*; most primitive *P. sardus* populations already attain big sizes also. Contrary to Western Mediterranean insular endemic glirids (Agustí, 1986), in insular endemic *Prolagus* species occlusal surface modifications appear even in the first phase of rapid evolution. As for hypsodonty



Species	Lenght (mm)
Prolagus vasconiensis	1.50
Prolagus ibericus	1.55
Prolagus tobieni	1.55
Prolagus oeningensis	1.60
Prolagus crusafonti	1.60
Ptychoprolagus forsthartensis	**1.70**
Prolagus vasc. fortis	1.81
Prolagus michauxi	1.85
Prolagus calpensis	1.97
Prolagus depereti	1.97
Prolagus major	**2.40**

Ptychoprolagus forsthartensis	**1.70**
Prolagus sardus	2.10
Prolagus aff. *P. depereti*	2.34*
Prolagus figaro	2.35
Prolagus major	**2.40**
Prolagus apricenicus	2.50
Prolagus imperialis	2.80

Fig. 7. P_3 size increase, hypsodonty increase and enamel folding should occur simultaneously (even if in a less or more marked way) to individuate an insular endemic *Prolagus* species. *P. major* (see text for details), a giant European continental species, is comparable in size to insular species, but shows no trace of enamel folding. On the other hand, in *Ptychoprolagus forsthartensis*, a high degree of enamel folding, but not an increase of the size (not so different from the primitive continental species *P. vasconiensis*) can be observed. Both size increase and enamel folding are evident on the occlusal surface of *P. imperialis*. Drawings from Ziegler & Fahlbusch (1986), Mazza (1987) and López Martínez (1989).
In the tables is reported P_3 average length in continental, non-endemic species (on the left) and insular endemic species (on the right). Length values of *Ptychoprolagus forsthartensis* and *P. major* are highlighted and reported in the right table too to better compare them with those of insular endemic species.
*Due to the scarcity of *Prolagus* aff. *P. depereti* dental elements, the reported length value is that of the figured specimen; the approximation is by defect as a consequence of its bad state of preservation.

Fig. 7. L'increment de la mida del P_3, l'increment de la hipsodòncia i del plegament de l'esmalt esdevenen simultàniament (tot i que en una forma més o menys marcada) a les espècies endèmiques insulars de Prolagus. P. major *(veure el text per detalls), una espècie europea continental gegant) és de mida comparable a les espècies insulars, però no mostra cap traça de plegament de l'esmalt. Per una altra banda, a* Ptychoprolagus forsthartensis, *hi ha un elevat grau de plegament de l'esmalt, però no es pot observar cap increment de la mida (no és gaire diferent de l'espècie continental primitiva* P. vasconiensis*). Tant l'increment de la mida com del grau de plegament de l'esmalt són evidents a la superfície oclusiva de* P. imperialis. *Dibuixos a partir de Ziegler & Fahlbusch (1986), Mazza (1987) and López Martínez (1989).*
A les taules es presenta la llargària promig del P_3 a espècies continentals no endèmiques (a l'esquerra) i espècies endèmiques insulars (a la dreta). Els valors de llargària de Ptychoprolagus forsthartensis *i* P. major *estan marcats i es registren a la taula dreta, per a que es puguin comparar millor amb els de les espècies insulars.*
**Degut a l'escassesa de materials dentaris de* Prolagus *aff.* P. depereti, *el valor de llargària presentat és el de l'espècimen il·lustrat; l'aproximació és per defecte, degut al mal estat de conservació.*

degree, it should decrease with the increasing complexity of occlusal surface, but data for "primitive" insular endemic species are not available.

A period of slow anagenesis following the first phase has been observed in Sardinia, where a cline of morphotypes in *P. sardus* populations have been individuated (Angelone *et al*, in prep.). A similar situation occurs in the Gargano archipelago: populations evolve increasing size and complexity even in a more clear and evident way than in *P. sardus*, but it is not clear if the appearance of *P. imperialis* is due to anagenesis or to archipelago effect (De Giuli *et al.*, 1986).

Evolutionary parallelism in dental morphology and size

In addition to size increase, the teeth of insular endemic micromammals show at least one of the following modifications:

1- molarization of premolars;

2- augmentation of the area of premolars (compared to extant elements of the tooth row);

3- appearance of additional crests or cusps;

4- increase of the enamel folding complexity;

5- absolute hypsodonty increase.

All of them represent different strategies directed to improve the efficiency of mastication, and they are a consequence of dietary and/or climatic adaptations (e.g.: herbivorous diet in glirids according to Mein, 1983; dry environments according to Agustí, 1986). Moreover, it is very likely that such modifications imply a change in the masticatory movements and consequently in the mandible mechanics.

Insular endemic *Prolagus* share three of the above listed feature (2, 4 and 5) with other micromammals that lived in Mediterranean insular environments. Such characters occur simultaneously, but not with the same evidence: for example, to a hypsodonty degree (I) increase usually does not correspond to an enamel folding complexity growth. It seems that to attain the purpose of improving mastication efficiency, one strategy prevails on the other rather than being combined: *P. imperialis*, for example, in which enamel folding complexity reaches its maximum degree, has a rather low hypsodonty degree (I) (tab. 1); in Sardinia and Corsica, the contrary happens for *P.* cf. *P. sardus* of Orosei fissure fillings, while *P. figaro*, showing a more complex enamel pattern, has a lower I value.

Environmental setting

Probably a change in dietary habits due to environmental/climatic changes and coping with harder vegetables can explain the above listed dental modifications. But that would imply that a same dry, open environmental setting was common to Western Mediterranean islands from Late Messinian on.

However, it should be emphasized that even in continental Europe, from Late Miocene on, a sudden change occurs in *Prolagus* size and morphology. As evidenced above (section: Results - Size increase) the appearance of *P. michauxi* represents a turning point in continental evolution of *Prolagus*, as this species starts acquiring some of the morpho-dimensional features till then exclusive of insular endemic species (even if never all together and in a lesser degree). The only plausible reason that justifies such an enormous morpho-dimensional shift is a climatic/environmental change: if so, on the analogy of insular endemic *Prolagus*, we should suppose an increase of aridity and of open spaces in continental Europe also starting from Late Miocene on. Further, advanced and exclusive modifications observed in *Prolagus* insular endemic species are due to the concurrent influence of climatic changes and insularity conditions.

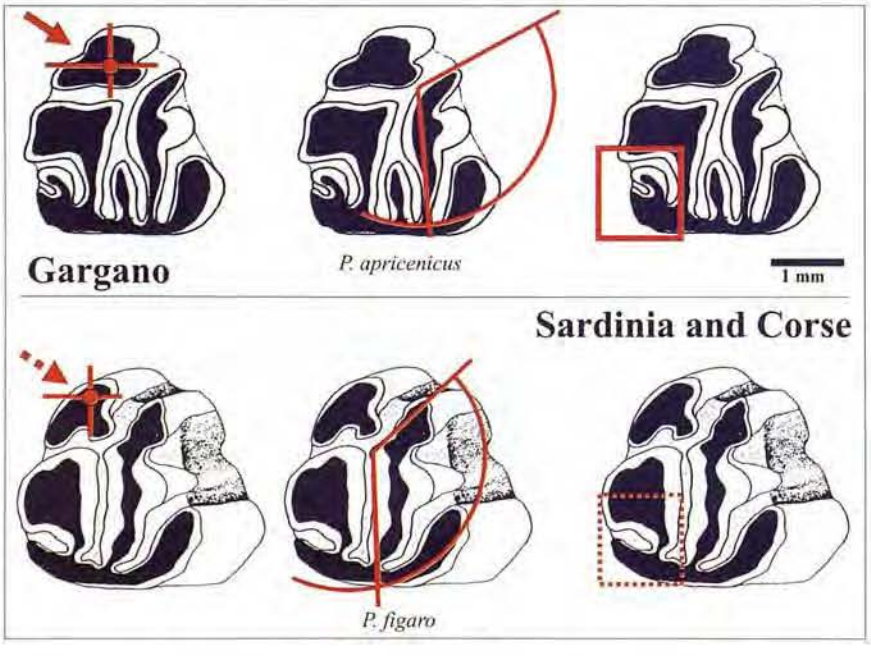


Fig. 8. Main differences between insular endemic *Prolagus* species of the Mediterranean area. Two groups have been distinguished: Gargano species (here represented by *P. apricenicus*) and Corso-Sardinian species (represented by *P. figaro*). Besides being bigger in size, Garganic species have a rectangular than a rather square shape (due to the anteroconid position), a lesser protoconid/protoconulid angle and a more complex and developed enamel folding. Drawings from López Martínez & Thaler (1975) and Mazza (1987).

Fig. 8. Diferències principals entre les espècies endèmiques insulars de Prolagus *de l'àrea mediterrània. S'han distingit dos grups: les espècies de Gargano (aquí representades per* P. apricenicus*) i les espècies corso-sardes (representades per* P. figaro*). Ademés de ser més grans, les espècies gargàniques tenen una forma més rectangular que quadrada (degut a la posició de l'anterocònid), un menor angle protocònid/protoconúlid i un desenvolupament més complex del plegament de l'esmalt. Dibuixos a partir de López Martínez & Thaler (1975) i Mazza (1987).*

Another explanation that could partly justify such changes could be a new dietary and/or ecological adaptation as a consequence of size increase, but it frankly is not very likely and it can not be demonstrated.

The peculiar characteristics attained by *P. michauxi* could in part explain why the difference between continental and insular species becomes less marked in Plio-Pleistocene times than in Mio-Pliocene times. Another reason could be the area of the Corso-Sardinian block, much bigger than the islands of the Garganic Mio-Pliocene archipelago, a factor that, influencing populations' size, could have prevented the developing of more marked morpho-dimensional modifications (Heaney, 1978).

Conclusions

Insular endemic *Prolagus* species have been found in Western Mediterranean area only. *Prolagus* species living in insular environments follow the micromammalian pattern of evolution on islands and undergo similar morpho-dimensional changes. It is by the simultaneous, more or less marked occurrence of such well defined morpho-dimensional modifications that they can be easily recognized. Those convergent features are shared by species that do not have a common direct ancestor: Gargano *Prolagus* species derive from *P. oeningensis*, a

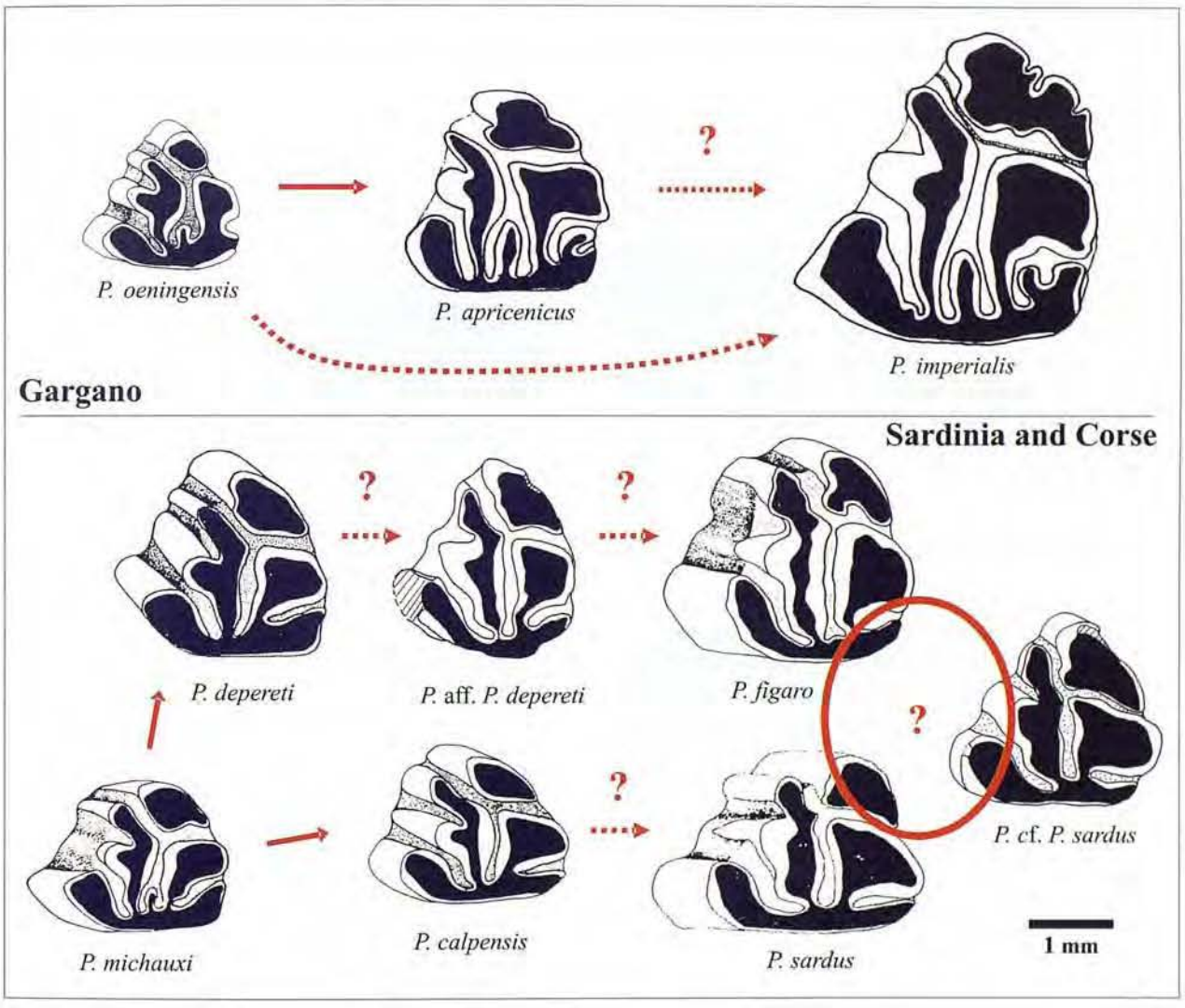


Fig. 9 – Phylogeny of insular endemic *Prolagus* species. *P. apricenicus* and *P. imperialis* descend from *P. oeningensis*, but it is not clear if they are part of an anagenetic lineage, or if they arose independently. Morphology and dimensions of *P. sardus* are very close to those of *P. calpensis*, while *P. figaro* closely resembles *P. depereti*. *Prolagus* aff. *P. depereti* shows intermediate morphologic features between the latter two species. Anyway, recent discoveries in the Monte Tuttavista area (Orosei, Eastern Sardinia, Italy; ?Late Pliocene-Upper Pleistocene) evidenced the existence of intermediate morphotypes between *P. figaro* and *P. sardus* (provisionally determined as *Prolagus* cf. *P. sardus*), opening again the discussion about the systematic of Corso-Sardinian *Prolagus* species. Drawings from López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) and from unpublished data of the author.

Fig. 9. Filogènia de les espècies endèmiques insulars de Prolagus. P. apricenicus *i* P. imperialis *deriven de* P. oeningensis, *però no està clar si formen part d'una línia anagenètica o si sorgeixen independentment. La morfologia i les dimensions de* P. sardus *són molt properes a les de* P. calpensis, *mentre que* P. figaro *s'assembla a* P. depereti. Prolagus *aff.* depereti *mostra unes característiques morfològiques intermèdies entre les de les dues darreres espècies. De totes formes, els descobriments recents a l'àrea del Monte Tuttavista (Orosei, Sardenya oriental, Itàlia; Pliocè superior? – Pleistocè superior) documenten l'existència de morfotipus intermedis (provisionalment determinats com a* P. *cf.* P. sardus*) entre* P. figaro *i* P. sardus, *obrint de nou la discussió sobre la sistemàtica de les espècies de* Prolagus *corso-sardes. Dibuixos a partir de López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) i de dades no publicades de l'autora.*

quite primitive European species, while the Corso-Sardinian species probably descend from one or two advanced species derived from the continental widespread *P. michauxi* (*P. calpensis* and/or *P. depereti*; López Martínez & Thaler, 1975; López-Martínez, 1978) (Fig. 9).

Increase of absolute and of relative size, of absolute hypsodonty and hypsodonty degree, of enamel folding complexity, reorganization of shape and relative position of occlusal surface elements on P_3 are the main elements that identify an insular endemic *Prolagus* species, to which should be added minor but significant modifications on the maxillary teeth in occlusion with P_3 (especially P^3). Such dental modifications probably involved significant changes in mandibular mechanics.

Almost all those characters can be related to mastication improving and therefore to a change of the diet. The most likely explanation for this phenomenon is a change of the environmental setting due to climatic changes.

The fact that all the above mentioned characters are related to chewing efficiency can also explain why they can not be observed in the same dental element with the same development degree: the result is a mosaic in which a mastication improving strategy prevails on the others that linger in a less developed stage. In Gargano species, for example, the tendency to enhance enamel folding complexity seem to prevail over a hypsodonty degree increase, the opposite seem to happen in Corso-Sardinian species. This distinction between Corso-Sardinian and Gargano species must be added to other differences in P_3 occlusal surface distinguishing the species of the two paleobioprovinces.

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In the last months, new fossil findings in the Monte Tuttavista karst fissure complex (Orosei, Eastern Sardinia, Italy) and the revision of Italian mainland *Prolagus* remains cast new light on the phylogeny of Corso-Sardinian species [Angelone, 2005: Systematic revision of genus *Prolagus* (Ochotonidae, Lagomorpha, Mammalia) in Italy and in Western Mediterranean Island: new systematic tools, biochronology and palaeogeography. Ph.D. Thesis, Università Roma Tre, 118 pp.]. Nevertheless, the morpho-dimensional and evolutionary observations made in this paper remain valid.

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